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The spatial scaling of beta diversity

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ABSTRACT

Beta diversity is an important concept used to describe turnover in species composition across a wide range of spatial and temporal scales, and it underpins much of conservation theory and practice. Although substantial progress has been made in the mathematical and terminological treatment of different measures of beta diversity, there has been little conceptual synthesis of potential scale-dependence of beta diversity with increasing spatial grain and geographic extent of sampling. Here, we evaluate different conceptual approaches to the spatial scaling of beta diversity, interpreted from 'fixed' and 'varying' perspectives of spatial grain and extent. We argue that a 'sliding window' perspective, in which spatial grain and extent covary, is an informative way to conceptualise community differentiation across scales. This concept more realistically reflects the varying empirical approaches that researchers adopt in field sampling and the varying scales of landscape perception by different organisms. Scale-dependence in beta diversity has broad implications for emerging fields in ecology and biogeography, such as the integration of fine-resolution eco-genomic data with large-scale macroecological studies, as well as for guiding appropriate management responses to threats to biodiversity operating at different spatial scales.

Keywords

Alpha diversity, community, differentiation, dissimilarity, gamma diversity, macroecology, spatial extent, spatial grain, Sørensen, species turnover

INTRODUCTION

Beta diversity is an important concept used in its broadest sense to describe variation in species identities from site to site (Anderson *et al.*, 2011). As a consequence, beta diversity is fundamental to community ecology and underpins conservation theory and practice (Gering *et al.*, 2003; Kraft *et al.*, 2011). The concept itself is often thought of in coarse (but intuitive) terms as 'species turnover'. Yet, a surprisingly wide variety of definitions and approaches to the analysis of beta diversity has emerged since Whittaker (1960) first introduced the concept. Since then, there has been an explosion of reviews and commentaries by diverse authors attempting to clarify important issues of analysis and terminology, with much recent success (e.g. Jost, 2007; Jurasinski *et al.*, 2009; Baselga, 2010b; Tuomisto, 2010b; Tuomisto, 2010a; Anderson *et al.*, 2011). Unfortunately, the same level of attention has not yet been given to other, equally fundamental, conceptual issues surrounding scale-dependence in the patterns and processes driving variation in beta diversity among sampling units at different spatial scales of observation, or among communities of organisms that perceive their environment at different spatial scales. As a consequence, there is as yet, no general framework for describing the spatial scaling of beta diversity.

Ecologists typically measure scale in terms of grain and extent (Nekola & White, 1999; Whittaker *et al.*, 2001). Within biogeography, there is extensive evidence for variation in the spatial patterns and processes driving alpha diversity at different spatial grain and extent (Palmer & White, 1994; Rosenzweig, 1995; Whittaker *et al.*, 2001; Field *et al.*, 2009). For example, at very fine scales, alpha diversity increases quickly with spatial extent due to high variation in stochastic species occupancy patterns among sampling units, and deterministic variation in species responses to habitat heterogeneity. At intermediate scales, diversity increases more slowly with spatial extent as fewer new species are encountered relative to the regional pool. Meanwhile, at very large scales, species diversity increases more quickly again across biogeographic regions with distinct geological barriers and evolutionary histories (Whittaker *et al.*, 2001; Hortal et al., 2010). Although there is recognition that spatial grain and extent also have important influences on the measurement and

70 interpretation of beta diversity (Nekola & White, 1999; Steinbauer *et al*., 2012), the patterns and
71 processes shaping the spatial scaling of beta diversity have not yet been thoroughly explored.
72 There are two main approaches that can be used to conceptualise spatial variation in beta
73 diversity: (i) the distance-decay of community similarity, and (ii) the partitioning of species
74 diversity into alpha and beta components. Distance-decay studies regress pair-wise measures of
75 sample-unit similarity against pair-wise spatial distance, and parameterise a 'slope' that indicates
76 the relative change in compositional similarity through geographic space (Nekola & White, 1999).
77 Diversity partitioning studies, meanwhile, derive aggregate measures of beta diversity (e.g.
78 Whittaker's (1960) multiplicative beta or Lande's (1996) additive beta) from the relationship
79 between mean alpha diversity in a sample-unit of a given grain versus gamma diversity from all
80 sampling units at their combined extent, and indicates the average diversity not found in any one
81 sampling unit (Veech & Crist, 2010). The effective number of compositionally-dissimilar sampling
82 units (the 'true' beta diversity of Tuomisto *et al*. 2010a) could be applied in a similar
83 (multiplicative) partitioning approach. When applied across multiple scales of sampling (i.e.
84 sampling units that are progressively aggregated upwards), diversity partitioning can thus give
85 insight into the scales at which beta diversity might be higher or lower.
86 A key difference between these two approaches is that the distance-decay relationship is
87 often used to describe directional turnover in species composition, and therefore could be viewed as
88 dissociating aggregate measures of beta diversity into a spatially explicit form. In contrast, diversity
89 partitioning need not be directional, and can give information about variation in species
90 composition among sampling units at different spatial scales. Both of these approaches have
91 advantages for addressing particular kinds of research questions (Anderson *et al.*, 2011). However,
92 recent work by Steinbauer *et al*. (2012) highlighted an important limitation of the distance-decay
93 approach when varying the grain or extent of sampling. Specifically, they showed in model
94 simulations with constant extent of study area, but increasing sample-unit size, that a low slope of
95 the distance-decay relationship may be found in contrasting situations of either very small sample-

96 unit size or very large sample-unit size. When sample-unit size is very small (relative to the study
97 area), even neighbouring sampling units may be very dissimilar due to high variability in species
98 occupancies, resulting in low decay in space. Meanwhile, when sample-unit size is very large, there
99 can be high similarity even between very distant sampling units due to an increased chance of
100 detecting species far from their spatial optima, thus resulting once again in low apparent decay in
101 space (but for very different reasons) (Steinbauer *et al*. 2012).

102 Given these considerations, the slope of the distance-decay function and the aggregate beta
103 measures obtained from diversity partitioning are not necessarily going to be telling the same story.
104 As Steinbauer *et al*. (2012) point out, the current spatially-explicit approaches used in distance-
105 decay functions are not robust enough to generalise across spatial scales.

106 In this paper, we take a diversity-partitioning approach to scaling and focus on the
107 interacting effects of grain and extent on aggregate measures of beta diversity. We explore different
108 approaches to conceptualising the effects of spatial scale on beta diversity, interpreted from 'fixed'
109 and 'varying' perspectives of spatial grain and extent, and discuss the implications of these for
110 understanding variation among communities of different organisms, and for targeting conservation
111 management at different spatial scales.

112

113 **THE IMPORTANCE OF SCALE**

114 Any putative scaling relationship will be intimately dependent on the spatial scales that are set, or
115 observed, for both alpha and gamma diversity. Absolute scales at which alpha and gamma diversity
116 should be measured have proven elusive. This is partly because ecologists have widely varying
117 objectives in addressing different research questions, and partly because species perceive and
118 respond to the world at widely varying spatial scales (Wiens, 1989; Palmer & White, 1994).
119 Consequently, alpha diversity is typically defined as the base sampling unit at a particular 'site'
120 (often representing the spatial grain of the study), while gamma diversity is defined as the sampling
121 area that is the aggregate of all sampling units (often representing the spatial extent of the study).

These choices of spatial grain and extent of sampling are (or at least should be) influenced by the biology of the particular taxon of interest, commonly the size or presumed dispersal capacity. For example, bacterial (Martiny *et al.*, 2011) and soil faunal communities (Nielsen *et al.*, 2010) are often quantified in sampling units of square centimetres, arthropod communities in sampling units of square metres (Kaspari *et al.*, 2010), and mammal communities in sampling units of square kilometres (Svenning *et al.*, 2011). In practice, there is also a strong tendency for spatial grain and extent to be positively correlated (co-varying across studies). This is because ecologists often aim to select a scale of field sampling that reflects the biology of the organisms being studied. Of course, ecological studies use a variety of data in addition to the direct sampling mentioned above. This includes checklists and atlases of species occurrences, which also will affect the spatial grain of the sampling units (Hortal, 2008).

It is tempting to see the choices made in the selection of spatial grain and extent as constraints on our ability to measure and interpret beta diversity. Indeed, this problem was highlighted by Nekola & White (1999), and also in the recent modelling study by Steinbauer *et al.* (2012), who suggested that the ecological mechanisms driving variation in distance-decay relationships may potentially be overshadowed by the effects of sampling at different spatial grains or study extents. For these reasons, a thorough understanding of the ways in which spatial grain and extent might affect observed patterns of beta diversity is critical for its proper interpretation. We suggest that a 'spatial window' of observation, defined by the spatial grain of sampling units and the spatial extent of the study area, is an appealing and informative prerequisite for developing any general model of the scaling of beta diversity. Our impression is that a 'spatial window' of observation is implicit in most (if not all) previous beta diversity studies, but has not been formalised explicitly into a model of spatial scaling.

In general terms, there are three ways in which this spatial window might vary, depending on the objectives of the study and the research questions being addressed. First, one might hold spatial grain constant while increasing spatial extent (Fig. 1a). This idea underpins the species-area

148 relationship, and might be used in the partitioning of species diversity for the same taxa across
149 geographic scales (Gering *et al.*, 2003). Second, one might hold spatial extent constant while
150 varying spatial grain (Fig. 1b), such as might occur when comparing samples of different taxa
151 sampled at different scales but within the same geographic area. Third, one might vary both spatial
152 grain and extent in the generalised case of a 'sliding window', such as when comparing samples of
153 different taxa taken at various spatial scales in different geographic areas (Fig. 1c).
154
155 **A GENERAL MODEL FOR THE SCALING OF BETA DIVERSITY**
156 Mechanistically, variation in diversity at local, regional or global scales is typically ascribed to
157 differing processes operating at different spatial scales (Table 1). These mechanisms can help
158 inform our *a priori* expectations for how beta diversity might vary among sampling units drawn at
159 each of these scales. In some cases, these expectations have been shown to coincide with a triphasic
160 form of the species-area relationship (Rosenzweig, 1995), which we use as a starting point for
161 discussion on the scaling of beta diversity (but note that our conclusions are not dependent on the
162 specific form that the SAR might take). Typically, species richness increases rapidly at local scales
163 as new sampling units are incorporated, due to high variation in stochastic species occupancy
164 patterns among sites, and deterministic variation in species responses to habitat heterogeneity
165 (Table 1). Beta diversity might therefore be expected to be high among sampling units drawn from
166 within local areas. At regional scales, species richness increases more slowly as fewer new species
167 are encountered relative to the regional pool. Consequently, beta diversity might be lower among
168 sampling units at regional scales, and the rate of increase from local scales might slow. At large
169 global scales, species richness increases again as new species are encountered across biogeographic
170 regions with distinct geological and evolutionary histories (Table 1). Therefore, beta diversity might
171 be higher among sampling units drawn from different continents than among sampling units drawn
172 from within a single region.

173 It is important to note that the 'beta diversity' we refer to here should not be considered
174 synonymous with the rate of change in alpha diversity across scales. Ideally, models of the spatial
175 scaling of beta diversity should reflect compositional dissimilarity that is statistically independent of
176 the 'true' number of communities sampled (*N*) and of species richness, as these two variables are
177 likely to change with spatial grain and extent. Whittaker's beta diversity, calculated as $\beta_W = \gamma / \alpha$, is
178 relatively insensitive to species richness but not to community number (Jost, 2007; Baselga, 2010a).
179 Thus, it is important to consider an appropriate normalized measure of differentiation to take
180 variation in the number of communities, or sampling units, into account. Such a measure is one
181 minus the multiple-site Sørensen index (Baselga, 2010b; Chao *et al.*, 2012). This can be interpreted
182 as the average among-sample dissimilarity at the specified scale, rather than an overall aggregate
183 measure, and is useful to consider when comparing across taxa or regions with varying levels of
184 richness and community number (Chao *et al.*, 2012).
185 We contrast these two measures of beta diversity, Whittaker's beta (β_W) versus one minus
186 the multiple-site Sørensen index ($\beta_{Sør}$), in our proposed scaling curves below to highlight the critical
187 importance of proper consideration of both community number and species richness. We adopt the
188 approach of Chao *et al.* (2012) in developing our conceptual scaling curves on the theoretical
189 assumption that *N* represents the number of 'true' communities with 'true' community parameters
190 of species richness and relative abundances (Chao *et al.*, 2012). We recognise that when scaling
191 curves are constructed from empirical samples, as will be necessary in practice, then the number of
192 sampling units will often incompletely represent the 'true' number of communities, and will require
193 standardisation by rarefaction or extrapolation (Colwell *et al.*, 2012). This must be considered prior
194 to the calculation of a normalised differentiation measure, such as one minus the multiple-site
195 Sørensen index (Chao *et al.*, 2012), and will improve comparability of beta diversity values across
196 different studies.
197 We combine the 'spatial window' concepts introduced in Fig 1 with the putative
198 mechanisms suggested to operate at different spatial scales described in Table 1, and propose a

199 series of conceptually different forms of the beta diversity scaling relationship, depending on
200 whether one takes a 'fixed' or 'varying' perspective of spatial grain and extent (Fig. 2). We suggest
201 that the form of these relationships is unlikely to be linear given the ecological mechanisms
202 operating across local to global scales (Table 1), and might well be logistic in form. Here, we
203 illustrate our arguments with a logistic form of the relationship (Fig. 2), but similar arguments could
204 be made with exponential, logarithmic, or even linear relationships.

205 The scaling relationships will also vary with the measure of beta diversity selected. First, we
206 describe potential scaling curves using an aggregate measure of Whittaker's multiplicative beta
207 diversity. If spatial grain is fixed and spatial extent is allowed to increase, then beta diversity will
208 naturally increase monotonically (Figs. 1a, 2a). Alternatively, if spatial extent is fixed and grain is
209 allowed to vary, then beta diversity might be expected to decrease monotonically (Figs. 1b, 2b).
210 That is, larger sample-unit areas will capture a larger portion of the community, and similarity
211 between sampling units will increase. If both grain and extent are allowed to vary across spatial
212 scales (a 'sliding window'), then beta diversity might be expected to follow a concave parabolic
213 scaling relationship (Figs. 1c, 2c), wherein dissimilarity among sampling units is higher at local and
214 global scales, but lower at regional scales.

215 The Whittaker's beta scaling relationships, however, do not account for differences in the
216 numbers of sampling units that are likely to occur at different spatial scales. At a comprehensive
217 level of sampling, the number of sampling units will intrinsically decline as spatial grain increases,
218 but increase as spatial extent increases. This will have a dramatic effect on the average 'per-sample'
219 differentiation indicated by one minus the multiple-site Sørensen index. Thus, when spatial grain is
220 small and spatial extent is large, very different values of beta diversity will be indicated by
221 Whittaker's beta compared with the multiple-site Sørensen index. We therefore show three
222 additional curves indicating the likely relationships observed for a normalised differentiation
223 measure such as one minus the multiple-site Sørensen index. What is immediately clear when using
224 this type of average among-sample dissimilarity measure of beta diversity is that the curves will

exhibit the opposite scaling relationships to that of Whittaker's beta diversity when either grain is fixed and extent varies (Fig 2d) or grain varies and extent is fixed (Fig 2e). Moreover, when extent is fixed at a large spatial scale, the increase in spatial grain is most likely to produce curves that approximate an exponential rather than logistic form (see dashed curves in Fig 2d and 2e). This implies that the shape of the scaling curves calculated from a normalised differentiation measure is unlikely to be the symmetrical opposite of its equivalent calculated from Whittaker's beta.

We reiterate that the logistic scaling relationship illustrated here is based on generalised assumptions about the underlying mechanisms detailed in Table 1. These assumptions, however, may not hold in all cases, and may not necessarily result in logistic beta scaling curves in all cases (particularly when using average among-sample dissimilarity measures of beta). We suggest that actual empirical scaling curves of beta diversity are likely to vary from simple linear to complex logistic relationships, depending on the range of spatial scales considered, the structure of the sampling design, the measure of beta diversity used, and the taxon or biogeographic areas being examined. Importantly, all underlying scaling assumptions for beta diversity appear to produce similar concave curves when grain and extent are allowed to co-vary using our 'sliding window' perspective (Fig 2c and 2f).

The three scaling approaches using the multiple-site Sørensen dissimilarity index outlined above (Fig 2 d, e, f) can be used to build a three-dimensional surface that shows the interactive effects of grain and extent on beta diversity across the full range of spatial scales (Fig. 3). Here, spatial grain and extent form the horizontal x- and y- axes, and beta diversity forms the vertical z-axis (Fig 3). At the extremes, as either grain or extent tend to zero, then beta will be logically undefined. Similarly, when grain equals extent, then beta diversity must be zero, as no differentiation among sampling units is possible. Between these logical bounds, we interpolate the remainder of the 3D surface based on the representation of Figures 2 d, e, and f as two-dimensional vertical 'slices' through the three-dimensional surface. An equivalent (but inversely-shaped) response surface could be represented for Whittaker's beta diversity. In essence, this reflects a

general form of the beta scaling relationship that might be expected for different study designs aimed at examining community turnover of different kinds of organisms, such as plants (Kraft *et al.*, 2011), vertebrates (Svenning *et al.*, 2011), or microbes (Martiny *et al.*, 2011) along various geographical or environmental gradients. The value of a more general conceptual model for the spatial scaling of beta diversity will be to synthesise across these disparate studies.

VARIATION IN THE SCALING OF BETA DIVERSITY ACROSS TAXA

Few studies on beta diversity have focused on more than one taxon (Ferrier *et al.*, 2004; Qian & Ricklefs, 2012). This has limited our appreciation of the importance of variation in the scaling of beta diversity across multiple and distinct taxa within and between ecological communities. There are few studies that explicitly compare patterns of beta diversity or endemism across disparate taxa, but evidence gained thus far suggests that divergent patterns exist. This may be because certain traits of organisms affect how they perceive and respond to their environment (Wiens, 1989) and how they are spatially distributed (Finlay *et al.*, 2006). Therefore, strong differences in trait complexes among different taxa, such as body size, niche width, and dispersal ability, are likely to strongly influence their response to spatial heterogeneity in the environment (Wiens, 1989; Nekola & White, 1999; Soininen *et al.*, 2007). For this reason, it is not surprising that studies have shown that species of large-bodied vertebrate taxa, for example, are often poor surrogates for species richness or endemicity of other taxa (Ferrier *et al.*, 2004; Schuldt & Assmann, 2010).

Regardless of which groups of organisms are compared, the scaling of beta diversity will not only be dependent on the spatial grain and extent of studies, but also on the traits of organisms being studied, and the environmental properties of the study environment (see Table 1). These ideas are also reflected in the 'everything is everywhere, but the environment selects' hypothesis, a topic of particular interest among microbial ecologists (Fontaneto, 2011). This debate centres on the relative roles of dispersal versus environmental selection in determining compositional variation through space, and thus levels of beta diversity at different spatial scales (Martiny *et al.*, 2011).

However, it also has broader implications for our understanding of the interaction between organism traits and geographic scale. For example, if we consider geographic range size as a surrogate for dispersal, and niche width as a surrogate for environmental selection, there are situations in which different taxa will display different levels of beta diversity. For example, host-specific parasites of large ungulates might have a narrow niche but a large geographic range size, whereas freshwater snails might have both a narrow niche and a small geographic range. In contrast, a generalist herbivore such as a locust, will have both a broad niche and large geographic range. But how do these different factors influence the shape of the scaling relationship for beta diversity?

The wide divergence in key ecological traits between taxa suggests that a single idealised form of the beta diversity scaling relationship will not be appropriate for all taxa. We outline three qualitative predictions that stem from our generalised form of the beta diversity scaling relationship, and explore how three key traits: (i) body size, (ii) resource use specialisation, and (iii) dispersal capacity might affect beta diversity at different spatial scales.

First, some groups of very small-bodied organisms, such as bacteria or protists, and to some extent insects, are vastly more numerous, diverse and compositionally heterogeneous than plants or vertebrates. Thus, a general scaling curve might change to show higher absolute beta diversity of communities of small organisms across the entire continuum of spatial scale relative to large-bodied organisms (prediction 1). Bacteria are several orders of magnitude smaller than insects, however, and consequently are small enough to be passively dispersed by air currents, for example. This means that some microbes actually have widespread distributions (Fontaneto, 2011), and even within groups of small organisms, there may be variation in potential beta diversity scaling curves Similarly, some migratory butterflies move hundreds of kilometres (Brower, 1961), and small insects are among the first organisms to colonise newly created volcanic islands (New, 2008). Size *per se* may therefore not necessarily predict dispersal capacity or range size, and therefore compositional turnover at different spatial scales.

303 Second, organisms will display very different resource use specialisation, and thus respond
304 to environmental heterogeneity at different spatial scales. For example, some generalist birds may
305 be able to persist in a wide variety of environments. Conversely, some arthropod groups will have
306 very narrow resource use specialisation and track environmental gradients at very fine spatial scales
307 (Kaspari *et al*., 2010; Nielsen *et al*., 2010). Thus, organisms with narrower resource specialisation
308 will tend to have greater heterogeneity of occurrence at a given scale than organisms with wide
309 resource use, such that a relatively small increase in the area sampled will result in a relatively rapid
310 accumulation of new species. Thus, for organisms with wide resource use, a general scaling curve
311 might change to show lower beta diversity values among fine-grained sampling units (prediction 2).
312 Third, dispersal capacity will affect the ability of organisms to colonise suitable
313 environments. Taxa with low average rates of dispersal might be expected to show lower average
314 geographic range sizes and higher rates of local endemism, resulting in higher rates of species
315 turnover at local to regional scales (Qian, 2009; Baselga *et al.*, 2012). For communities with a high
316 proportion of dispersal limited species, a general scaling curve might therefore be expected to show
317 higher beta diversity values at small spatial scales (prediction 3).
318 In reality, there is strong covariance in traits across phylogenetic lineages (Harvey & Pagel,
319 1991), and we would expect taxa with distinct suites of size, dispersal or resource specialisation
320 traits to produce different relative forms of the beta scaling relationship. It might be generalised, for
321 example, that scaling relationships for some groups of organisms with small body size, narrow
322 resource preference and low dispersal capacity will be quite different than for large, dispersive
323 generalist species. We expect that the effect of these types of trait differences on the precise form of
324 the beta diversity scaling relationship will be fertile ground for further empirical testing.
325
326 **IMPLICATIONS**
327 Our perspective on the spatial scaling of beta diversity will have important implications in many
328 areas of ecology, including (i) the linking of macroecology with phylogeography and ecogenomics,

329 (ii) the design of new studies to understand community assembly at different scales, and (iii) the
330 conceptual underpinning of multi-scale biodiversity management.

331 First, dramatic reductions in the cost of gene sequencing are enabling much finer-grained
332 assessment of microbial biodiversity across regions than ever before (Poole *et al.*, 2012). This has
333 broad implications for the integration of emerging fields, such as ecogenomics, with traditional
334 macroecological studies. In the near future, we can envisage this filling a significant gap in the
335 incorporation of fine-grained empirical data into macroecological studies over large spatial extents
336 (Beck *et al.*, 2012). Such integration may have further implications for phylogeography, and could
337 provide new insights into processes driving community differentiation and endemism through space
338 and time (Schmidt *et al.*, 2011).

339 Second, it is well established that different factors affect community assembly at different
340 scales. For example, climate and historical factors can act as large scale filters, whereas habitat
341 structure and dispersal can act as local filters on community assembly (see Table 1). Our 'sliding
342 window' perspective on spatial grain and extent may provide a useful framework to design new
343 studies, or meta-analysis of pre-existing datasets, to examine the relative effects of multiple filters
344 on community assembly, and thus beta diversity, across multiple scales (Rajaniemi *et al.*, 2006;
345 Wang *et al.*, 2009).

346 Third, if beta diversity scaling relationships vary widely across disparate organisms, then
347 conservation strategies will need to focus more explicitly on the requirements of multiple taxa at
348 multiple spatial scales to prevent the loss of species (Lindenmayer & Franklin, 2002). Any credible
349 plan for biodiversity conservation must maintain beta diversity (and the processes that shape it)
350 across the full range of taxa and spatial scales. The only way to achieve this will be through multi-
351 scaled conservation approaches (Lindenmayer & Franklin, 2002). At present, conservation
352 management is generally planned at 'regional' scales (Ferrier *et al.*, 2004) and implemented for a
353 small subset of biodiversity (typically vertebrates and plants) at 'local' scales (Bestelmeyer *et al.*,
354 2003). These local scales are almost invariably defined at human-perceived spatial grains within

landscapes (e.g. field or farm scales), which do not match the spatial scales of perception of the majority of organisms that are much smaller in size (Manning *et al.*, 2004). Although there are some examples of reserves being created for threatened insect species (Brereton *et al.*, 2008; Watts & Thornburrow, 2009), and some consideration of insects in conservation planning at multiple scales (Cabeza *et al.*, 2010), there are limited examples of active management that considers the fine grained niche requirements of insect species within landscapes. Some examples where this has occurred include the enhancement of food resources within a forestry context (Gibb *et al.*, 2006), addition of microhabitat complexity within a restoration context (Barton *et al.*, 2011), or the planting of field margins in agricultural contexts (Pywell *et al.*, 2011). By contrast, most management interventions at larger scales, such as tree plantings, may enhance only the perceived 'quality' of habitat for a subset of vertebrates species at landscape scales (Cunningham *et al.*, 2007). This may have limited or no effect on some groups of organisms that perceive and respond to plant composition at finer spatial scales (Tylianakis *et al.*, 2006; Barton *et al.*, 2010). This is not to say that management intervention at landscape scales is unimportant. Rather, interventions leading to an improvement in fine-scale habitat conditions within sites that are subsets of the larger landscape are more likely to affect the composition of diverse arthropod assemblages than landscape-scale interventions. In this sense, management interventions at different spatial scales should be seen as complementary, as they affect different suites of taxa.

CONCLUSIONS

By establishing some expectations for how beta diversity varies across spatial scales, the critical role that sampling and study design plays, and how these patterns might vary with organism traits, we hope to stimulate development of a more general framework for testing the processes structuring communities and ecosystems. This has broad implications for the integration of emerging fields, such as ecogenomics with traditional macroecological studies. We suggest there are also significant opportunities for conservation managers to make biodiversity gains if the spatial scaling of beta

diversity is properly considered across different taxa with contrasting traits, and incorporated into management actions at multiple spatial scales. High habitat specificity and poor dispersal ability are characteristics favour speciation and compositional turnover, but which are not typical of the charismatic vertebrates for which many reserve systems are designed. We argue that a greater understanding of the spatial scaling of beta diversity will be crucial for improving conservation theory and practice. Exploring the conceptual underpinnings of the spatial scaling of beta diversity will enable a deeper integration of biodiversity phenomena at vastly different scales and across distinct groups of organisms.

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BIOSKETCH

Philip Barton is a research fellow at the Fenner School of Environment and Society, Australian National University. His research focuses on examining the spatial and temporal drivers of insect, plant and vertebrate community dynamics and its application to ecosystem restoration and biodiversity conservation. PB, SC and RD conceived the main ideas, and all authors contributed to their development. PB and RD wrote the paper, with comments from all authors.

REFERENCES

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C.

& Swenson, N. G. (2011) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19-28.

Barton, P. S., Manning, A. D., Gibb, H., Lindenmayer, D. B. & Cunningham, S. A. (2010) Fine-scale heterogeneity in beetle assemblages under co-occurring *Eucalyptus* in the same subgenus. *Journal of Biogeography*, **37**, 1927-1937.

Barton, P. S., Manning, A. D., Gibb, H., Wood, J. T., Lindenmayer, D. B. & Cunningham, S. A. (2011) Experimental reduction of native vertebrate grazing and addition of logs benefit beetle diversity at multiple scales. *Journal of Applied Ecology*, **48**, 943-951.

Baselga, A. (2010a) Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. *Ecology*, **91**, 1974-1981.

Baselga, A. (2010b) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134-143.

Baselga, A., Lobo, J. M., Svenning, J. C., Aragón, P. & Araújo, M. B. (2012) Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles. *Global Ecology and Biogeography*, in press.

Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, J., Fritz, S. A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M. & Dormann, C. F. (2012) What's on the horizon for macroecology? *Ecography*, **early view**, doi: 10.1111/j.1600-0587.2012.07364.x.

Bestelmeyer, B. T., Miller, J. R. & Wiens, J. A. (2003) Applying species diversity theory to land management. *Ecological Applications*, **13**, 1750-1761.

Brereton, T. M., Warren, M. S., Roy, D. B. & Stewart, K. (2008) The changing status of the Chalkhill Blue butterfly Polyommatus coridon in the UK: the impacts of conservation policies and environmental factors. *Journal of Insect Conservation*, **12**, 629-638.

Brower, L. P. (1961) Studies on migration of Monarch butterfly.1. Breeding populations of *Danaus plexippus* and *D gilippus berenice* in south central Florida. *Ecology*, **42**, 76-83.

433 Cabeza, M., Arponen, A., Jaattela, L., Kujala, H., Van Teeffelen, A. & Hanski, I. (2010)
434 Conservation planning with insects at three different spatial scales. *Ecography*, **33**, 54-63.
435 Chao, A., Chiu, C.-H. & Hsieh, T. C. (2012) Proposing a resolution to debates on diversity
436 partitioning. *Ecology*, **in press**.
437 Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S.-Y., Mao, C. X., Chazdon, R. L. & Longino, J. T.
438 (2012) Models and estimators linking individual-based and sample-based rarefaction,
439 extrapolation and comparison of assemblages. *Journal of Plant Ecology*, **5**, 3–21.
440 Cunningham, R. B., Lindenmayer, D. B., Crane, M., Michael, D. & Macgregor, C. (2007) Reptile
441 and arboreal marsupial response to replanted vegetation in agricultural landscapes. *Ecological*
442 *Applications*, **17**, 609-619.
443 Ferrier, S., Powell, G. V. N., Richardson, K. S., Manion, G., Overton, J. M., Allnutt, T. F.,
444 Cameron, S. E., Mantle, K., Burgess, N. D., Faith, D. P., Lamoreux, J. F., Kier, G., Hijmans,
445 R. J., Funk, V. A., Cassis, G. A., Fisher, B. L., Flemons, P., Lees, D., Lovett, J. C. & Van
446 Rompaey, R. (2004) Mapping more of terrestrial biodiversity for global conservation
447 assessment. *Bioscience*, **54**, 1101-1109.
448 Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. a. F., Guegan, J. F.,
449 Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'brien, E. M. & Turner, J. R.
450 G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of*
451 *Biogeography*, **36**, 132-147.
452 Finlay, B. J., Thomas, J. A., Mcgavin, G. C., Fenchel, T. & Clarke, R. T. (2006) Self-similar
453 patterns of nature: insect diversity at local to global scales. *Proceedings of the Royal Society*
454 *B-Biological Sciences*, **273**, 1935-1941.
455 Fontaneto, D. (2011) *Biogeography of micro-organisms. Is everything small everywhere?*, edn.
456 Cambridge University Press.

457 Gering, J. C., Crist, T. O. & Veech, J. A. (2003) Additive partitioning of species diversity across
458 multiple spatial scales: Implications for regional conservation of biodiversity. *Conservation*
459 *Biology*, **17**, 488-499.
460 Gibb, H., Hjälten, J., Ball, J. P., Atlegrim, O., Pettersson, R. B., Hilszczanski, J., Johansson, T. &
461 Danell, K. (2006) Effects of landscape composition and substrate availability on saproxylic
462 beetles in boreal forests: a study using experimental logs for monitoring assemblages.
463 *Ecography*, **29**, 191-204.
464 Harvey, P. H. & Pagel, M. D. (1991) *The comparative method in evolutionary biology.*, edn. Oxford
465 University Press, New York, USA.
466 Hortal, J. (2008) Uncertainty and the measurement of terrestrial biodiversity gradients. *Journal of*
467 *Biogeography*, **35**, 1335-1336.
468 Hortal, J., Roura-Pascual, N., Sanders, N. J. & Rahbek, C. (2010) Understanding (insect) species
469 distributions across spatial scales. *Ecography*, **33**, 51-53.
470 Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**,
471 2427-2439.
472 Jurasinski, G., Retzer, V. & Beierkuhnlein, C. (2009) Inventory, differentiation, and proportional
473 diversity: a consistent terminology for quantifying species diversity. *Oecologia*, **159**, 15-26.
474 Kaspari, M., Stevenson, B. S., Shik, J. & Kerekes, J. F. (2010) Scaling community structure: how
475 bacteria, fungi and ant taxocences differentiate along a tropical forest floor. *Ecology*, **91**,
476 2221-2226.
477 Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J.
478 C., Vellend, M., Boyle, B., Anderson, M. J., Cornell, H. V., Davies, K. F., Freestone, A. L.,
479 Inouye, B. D., Harrison, S. P. & Myers, J. A. (2011) Disentangling the drivers of beta
480 diversity along latitudinal and alevational gradients. *Science*, **333**, 1755-1758.
481 Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple
482 communities. *Oikos*, **76**, 5-13.

Lindenmayer, D. B. & Franklin, J. F. (2002) *Conserving forest biodiversity: A comprehensive multi-scaled approach.*, edn. Island Press, Washington.

Manning, A. D., Lindenmayer, D. B. & Nix, H. A. (2004) Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos*, **104**, 621-628.

Martiny, J. B. H., Eisen, J. A., Penn, K., Allison, S. D. & Horner-Devine, M. C. (2011) Drivers of bacterial beta-diversity depend on spatial scale. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 7850-7854.

Nekola, J. C. & White, P. S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867-878.

New, T. R. (2008) Insect conservation in early succession on islands: lessons from Surtsey, Iceland, and the Krakatau Archipelago, Indonesia. *Journal of Insect Conservation*, **12**, 307–312.

Nielsen, U. N., Osler, G. H. R., Campbell, C. D., Neilson, R., Burslem, D. & Van Der Wal, R. (2010) The enigma of soil animal species diversity revisited: the role of small-scale heterogeneity. *PLoS ONE*, **5 (7)**, e11567.

Palmer, M. W. & White, P. S. (1994) Scale dependence and the species-area relationship. *American Naturalist*, **144**, 717-740.

Poole, A. M., Stouffer, D. B. & Tylianakis, J. M. (2012) 'Ecosystomics': ecology by sequencer. *Trends in Ecology & Evolution*, **27**, 309-310.

Pywell, R. F., Meek, W. R., Loxton, R. G., Nowakowski, M., Carvell, C. & Woodcock, B. (2011) Ecological restoration on farmland can drive beneficial functional responses in plant and invertebrate communities. *Agriculture Ecosystems & Environment*, **140**, 62-67.

Qian, H. (2009) Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, **18**, 327-332.

Qian, H. & Ricklefs, R. E. (2012) Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography*, **21**, 341-351.

509 Rajaniemi, T. K., Goldberg, D. E., Turkington, R. & Dyer, A. R. (2006) Quantitative partitioning of
510 regional and local processes shaping regional diversity patterns. *Ecology Letters*, **9**, 121-128.
511 Ricklefs, R. E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology*
512 *Letters*, **7**, 1-15.
513 Rosenzweig, M. L. (1995) *Species diversity in space and time*, edn. Cambridge University Press.
514 Schmidt, S. K., Lynch, R. C., King, A. J., Karki, D., Robeson, M. S., Nagy, L., Williams, M. W.,
515 Mitter, M. S. & Freeman, K. R. (2011) Phylogeography of microbial phototrophs in the dry
516 valleys of the high Himalayas and Antarctica. *Proceedings of the Royal Society B-Biological*
517 *Sciences*, **278**, 702-708.
518 Schuldt, A. & Assmann, T. (2010) Invertebrate diversity and national responsibility for species
519 conservation across Europe - A multi-taxon approach. *Biological Conservation*, **143**, 2747-
520 2756.
521 Soininen, J., Lennon, J. J. & Hillebrand, H. (2007) A multivariate analysis of beta diversity across
522 organisms and environments. *Ecology*, **88**, 2830-2838.
523 Steinbauer, M., Dolos, K., Reineking, B. & Beierkuhnlein, C. (2012) Current measures for distance
524 decay in similarity of species composition are influenced by study extent and grain size.
525 *Global Ecology and Biogeography*, DOI: 10.1111/j.1466-8238.2012.00772.x.
526 Svenning, J. C., Fløjgaard, C. & Baselga, A. (2011) Climate, history and neutrality as drivers of
527 mammal beta diversity in Europe: insights from multiscale deconstruction. *Journal of Animal*
528 *Ecology*, **80**, 393-402.
529 Tuomisto, H. (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1.
530 Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2-22.
531 Tuomisto, H. (2010b) A diversity of beta diversities: straightening up a concept gone awry. Part 2.
532 Quantifying beta diversity and related phenomena. *Ecography*, **33**, 23-45.

533 Tylianakis, J. M., Klein, A. M., Lozada, T. & Tscharntke, T. (2006) Spatial scale of observation
534 affects alpha, beta and gamma diversity of cavity-nesting bees and wasps across a tropical
535 land-use gradient. *Journal of Biogeography*, **33**, 1295-1304.
536 Veech, J. A. & Crist, T. O. (2010) Toward a unified view of diversity partitioning. *Ecology*, **91**,
537 1988-1992.
538 Wang, X. P., Fang, J. Y., Sanders, N. J., White, P. S. & Tang, Z. Y. (2009) Relative importance of
539 climate vs local factors in shaping the regional patterns of forest plant richness across
540 northeast China. *Ecography*, **32**, 133-142.
541 Watts, C. & Thornburrow, D. (2009) Where have all the weta gone? Results after two decades of
542 transferring a threatened New Zealand giant weta, Deinacrida mahoenui. *Journal of Insect*
543 *Conservation*, **13**, 287-295.
544 Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological*
545 *Monographs*, **30**, 279-338.
546 Whittaker, R. J., Willis, K. J. & Field, R. (2001) Scale and species richness: towards a general,
547 hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.
548 Wiens, J. A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385-397.

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552 **Table 1**. A variety of different occupancy, bionomic, and biogeographic factors are suggested to
553 drive beta diversity at different spatial scales (Whittaker *et al.*, 2001; Ricklefs, 2004; Hortal *et al.*,
554 2010).

Spatial scales	**Scale of beta diversity**	**Examples of environmental factors**	**Examples of organismal factors**
Local $< 10^6$ m^2	Heterogeneity within and between habitat patches	Habitat composition and structure, soils, disturbance	Stochastic occupancy, species interactions, resource specificity, niche requirements
Regional $10^6 – 10^{10}$ m^2	Differences in communities across landscapes and large geographic areas within continents	Topology, altitude, discontinuous habitat, latitudinal gradients in productivity and climate, energy dynamics	Dispersal limitation, trophic position, range size, meta-community dynamics
Global $>10^{10}$ m^2	Variation in evolutionary history across biogeographic regions	Isolation by mountain ranges, continental isolation, plate tectonics	Speciation-extinction events, higher taxon replacement

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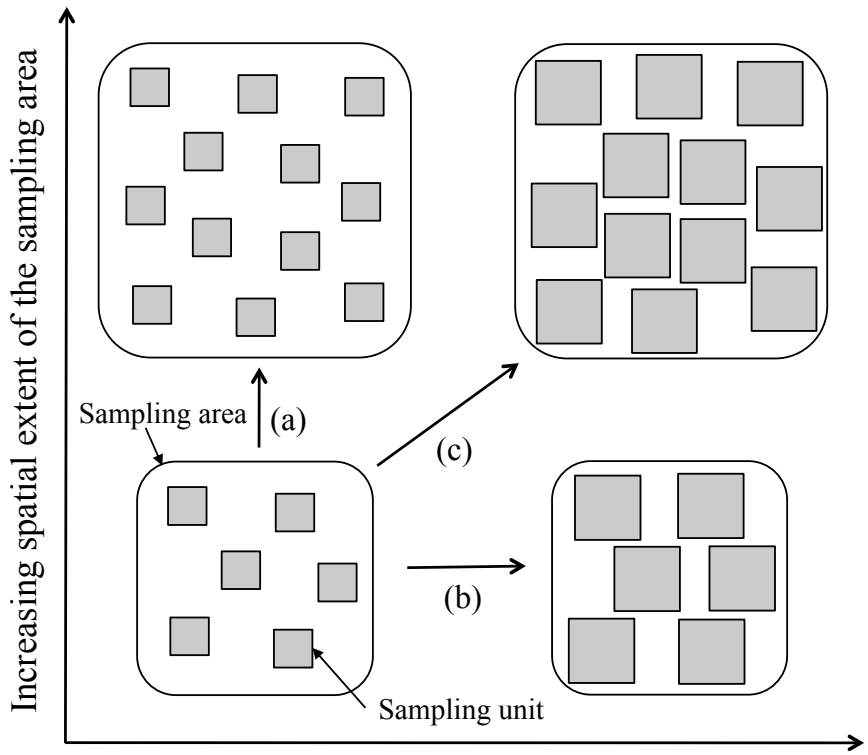

558

559 **Figure 1.** Interpretation of scale-dependence in ecological phenomena depends sensitively on how
560 the spatial grain of sampling units and the spatial extent of the sampling area are defined and scaled
561 (after Anderson *et al*. 2011). The ways in which spatial grain and extent may scale include (a)
562 fixing the spatial grain of the sampling unit and varying the spatial extent of the sampling area, (b)
563 fixing extent and varying the spatial grain of the sampling units, or (c) varying both spatial grain
564 and extent together, giving a 'sliding window' of spatial observation.

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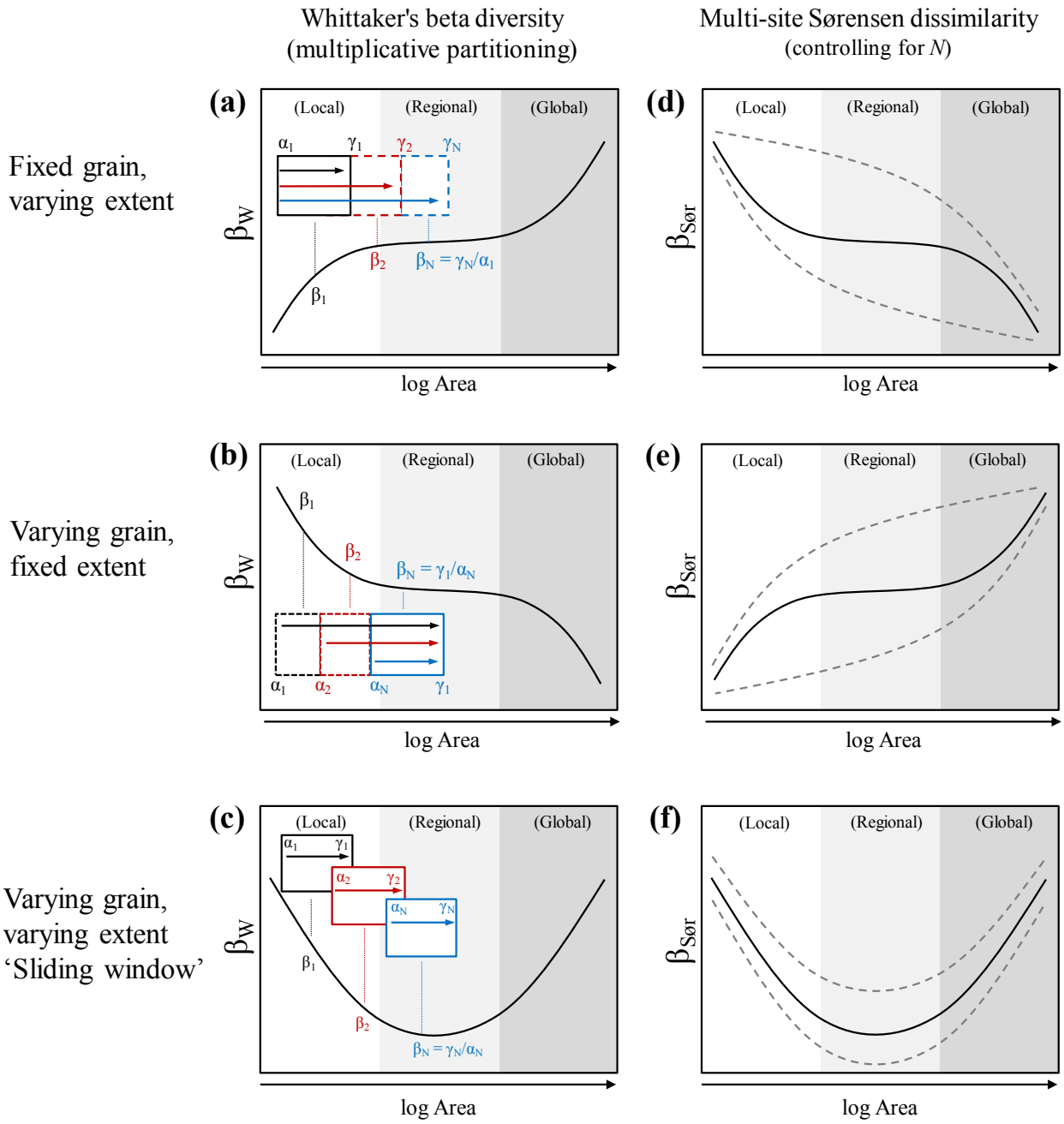

Figure 2. Conceptual approaches to the spatial scaling of β-diversity can be derived from the interaction between sampling grain and study extent, which define the 'spatial window' of observation. The spatial grain of sampling units will define the scale of α-diversity, and the spatial extent of a study will define the scale of γ-diversity. However, different measures of beta diversity will produce different scaling curves. For a purely aggregate measure such as Whittaker's multiplicative beta ($\beta_W = \gamma/\alpha$), then β-diversity will: (a) increase monotonically if the spatial scale of α-diversity is fixed but the scale of γ-diversity is allowed to vary; (b) decrease monotonically if

575 the spatial scale of γ-diversity is fixed, but the scale of α-diversity is allowed to vary; and (c) exhibit
576 a concave parabolic curve if the spatial scales of both α and γ vary together (a 'sliding window').
577 Aggregate measures of beta can be confounded by the number of sampling sites (*N*) compared,
578 which intrinsically decline as spatial grain increases, but increase as spatial extent increases. A
579 normalised measure of beta that controls for N, such as one minus the multiple-site Sørensen
580 similarity index (β_{Sor}), will produce curves in the opposite direction to Whittaker's beta diversity
581 when either (d) grain, or (e) extent is fixed, representing the change in average dissimilarity among
582 sampling units at that scale. The logistic scaling relationship illustrated here is based on generalised
583 assumptions about the underlying mechanisms detailed in Table 1. These assumptions, however,
584 may not hold in all cases, and we suggest that actual empirical scaling curves of beta diversity are
585 likely to vary from simple linear to complex logistic relationships (dashed lines in (d), (e), and (f)),
586 depending on the range of spatial scales considered, the structure of the sampling design, the
587 measure of beta diversity, and the taxon or biogeographic areas being examined. Importantly, both
588 measures of beta diversity will produce the same concave curve when grain and extent are allowed
589 to co-vary using our 'sliding window' perspective (c) and (f).
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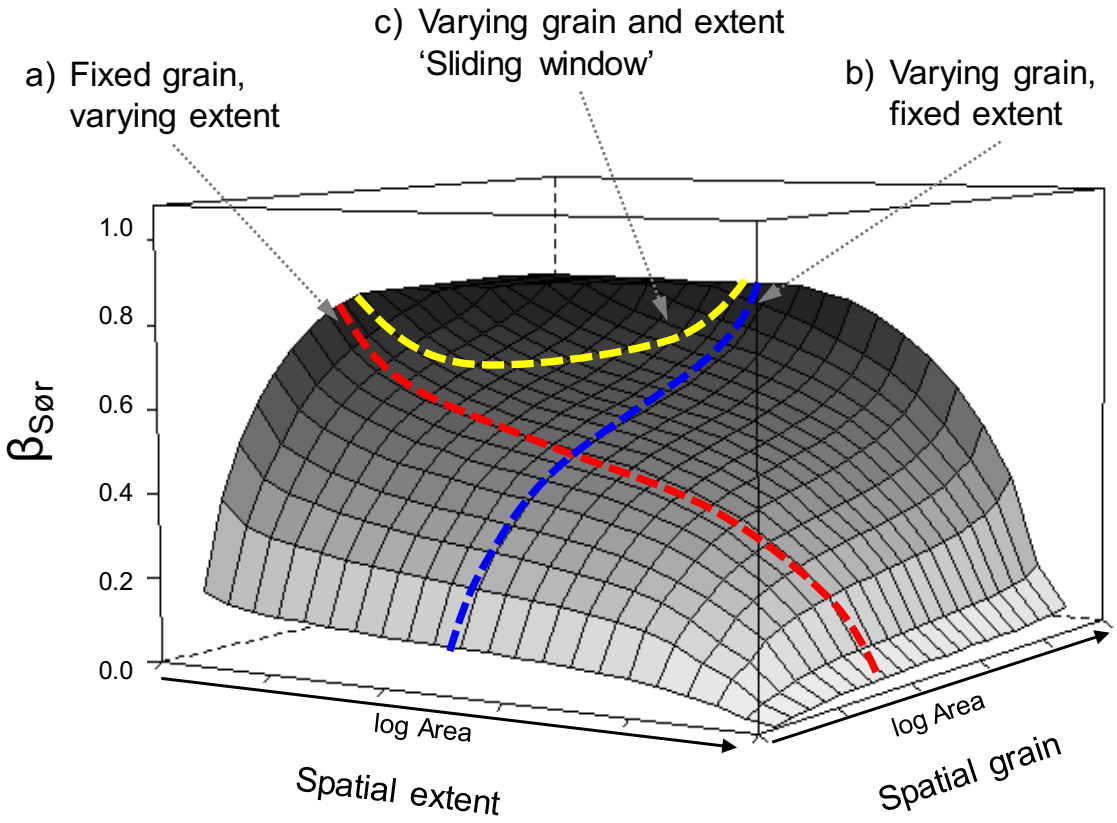

591

592 **Figure 3.** A general conceptual model for the spatial scaling of beta diversity. The three-
593 dimensional surface shows schematically how varying spatial scales of sampling grain and study
594 extent might influence beta diversity. Here, 'beta diversity' is depicted on the vertical axis as one
595 minus the multiple-site Sørensen index (Baselga, 2010b; Chao *et al.*, 2012), but alternative scaling
596 relationships could be depicted for Whittaker's beta (Whittaker, 1960), the effective number of
597 compositionally-dissimilar sampling units (Tuomisto, 2010a), or other metrics. The surface
598 interpolates between three two-dimensional 'slices' that represent conceptually different forms of
599 the beta scaling relationship, depending on whether (a) grain is fixed and extent is allowed to vary,
600 (b) extent is fixed and grain is allowed to vary, or (c) grain and extent are allowed to vary together
601 in the sense of a 'sliding window' of spatial observation.

602